Selection in Natural Populations

Reproductive Success. Studies of Individual Variation in Contrasting Breeding Systems. T. H. CLUTTON-BROCK, Ed. University of Chicago Press, Chicago, 1988. x, 538 pp., illus. $75; paper, $29.95.

Natural selection depends upon variation in reproductive success (fitness) among individuals in populations. Evolutionary response follows upon selection when traits that influence reproductive success are inherited. For many years, the study of natural selection was largely confined to theoretical assessments of the behavior of a small number of loci and to programs of "artificial" selection on targeted traits of laboratory and domesticated animals, where selection could be controlled by the investigator. Recently, however, several biologists, notably M. J. Wade, R. Lande, and S. J. Arnold at Chicago and J. A. Endler at Santa Barbara, have developed and popularized a generalized measure of actual or potential strength of selection in natural populations. In comparisons among populations, the potential for natural selection (I) may be estimated by the ratio of the variance in reproductive success to the square of its mean (hence, the square of the coefficient of variation). The ratio I(males)/I(females) quantifies potential for sexual selection on males.

Although more complex in detail, such a simple representation inevitably invites application, and coincidentally with the recent theoretical developments the culmination of several detailed, long-term studies of natural populations has seemingly produced the data required. Though some of the more recent studies were undertaken to measure potential selection, the older ones, some of them dating from the 1940s and 1950s, were initiated to investigate population regulation, compile actuarial statistics of long-lived organisms, and interrelate familial lineages and social interactions within populations.

Reproductive Success expresses a happy union of theory and empiricism in an important collection of essays. The authors of 25 of these have fit their field data on particular populations (5 insect, 1 amphibian, 13 bird, and 6 mammal) to the paradigm of potential selection. An introduction and three concluding chapters by Clutton-Brock, David Brown, and Alan Grafen address general issues. Each of the authors of empirical chapters was asked, to the extent possible given limitations of data, to calculate selection potentials and estimate the magnitude of their components deriving from variation in survival to breeding age, reproductive lifespan, fecundity (females) or mating success (males), and offspring survival to independence. Brown explains a commonly used technique to accomplish this. In addition, most of the studies related reproductive success to individual traits, particularly age, size, and experience, and to environmental variables.

Mathematically, fitness is closely associated with lifetime reproductive success (LRS). Although one may estimate components of LRS in short-term, cross-sectional studies, Clutton-Brock advocates longitudinal investigations, that is, of individuals followed throughout their lives. Longitudinal data allow one to estimate age effects and to eliminate the confounding effects of correlations between fecundity and mortality rate. Such data often are acquired with difficulty. In George Dunnet's study of fulmars, some of his inaugural subjects in 1951 were still breeding in 1984, attesting to the perseverance of both seabirds and their investigators and to the uniqueness of the information presented in *Reproductive Success*.

The individual chapters themselves are treasuries of natural history of organisms as diverse as damselflies (Fincke) and elephant seals (Le Boeuf and Reiter). We learn that among adult female sparrowhawks, LRS varied between 0 and 23 offspring, with 3 and 4 being the commonest non-zero values; but of female fledglings just independent of parental care 72% did not survive to reproduce (Newton). In Howard's study of frogs, reproductive success increases with size as females produce more and larger eggs and males gain more matings with larger females. Among male black grouse, number of copulations per season varied between 0 and 20; success was markedly higher in middle age (3 to 5 years) than in youth or old age (Kruijt and de Vos). Experience and senescence also express themselves in male reproductive success of harem-forming mammals (red deer [Clutton-Brock, Albon and Guinness] and elephant seals) in which males vie among each other for ownership of females. Intra-male competition, which may include infanticide by male lions newly joining social groups (Packer *et al.*), tends to increase values of I for males compared to those for females, establishing the potential for sexual selection.

Closer to home, whereas older individuals of many mammal species fail to gain matings, in one African human society reproductive success increases into old age as an individual's wealth accumulates (Borgerhoff Mulder). That society condones and even codifies the accumulation and inheritance of culturally derived fitness is a remarkable aspect of human nature, perhaps attesting to the ascendancy of family fitness over individual fitness in large, stable social groups. In studies of birds, offspring helping to rear their siblings did not appear to increase the LRS of scrub jays (Fitzpatrick and Woofenden), but communal breeding reduced mortality of adult anis (cuckoo family) by partially emancipating them from incubation duty at nests vulnerable to predators (Vehrencamp, Koford, and Bowen). Even mutualistic interactions between species may be important: in one species of lycaenid butterfly, males recognize high-quality females, and thereby enhance their mating success, by the number of their ant attendants (Elgar and Pierce).

As in any broadly comparative project, diversity permeates the fabric of observations that constitute this book. In the final chapter, however, Clutton-Brock discerns general patterns. First, the potential for selection (I) depends upon the stage of the life cycle at which reproductive output is estimated—zygotes, offspring reared to independence, and young recruited into the breeding population. For females, median values of I were approximately 0.4, 0.7, and 1.4 at these stages; for males, they were 1.1, 0.9, and 1.4. Evidently, parental and early environmental influences linger long after independence. Values of I estimated from variance in numbers of zygotes and young indicate potential for sexual selection on males, but this disappears when survival of immatures enters the equation for fitness.

In many random processes, such as the Poisson, variances in distributions equal the mean. Thus values of I deviating from 1 suggest nonrandom distribution of LRS or covariances between components of LRS. The studies in *Reproductive Success* revealed seven cases of positive covariance between fecundity and longevity, indicating variation in traits affecting fitness components generally; conversely, there surfaced only three weak negative covariances, providing little evidence of trade-offs between life-history components. Chance plays a prominent role in LRS; whether a kittiwake survives to breed once or ten times depends partly on luck. Some of the variance in LRS was clearly associated with age, body size, social

dominance—themselves partly inherent and partly chance—and impositions of the environment.

I liked this book. The empirical chapters are informative and well written. Clutton-Brock's thoughtful remarks articulate the common themes of *Reproductive Success*. However, lest I leave the impression that the study of selection in natural populations is inexorably bound on the road to fulfillment, I must recount several problems, to which the contributors themselves frequently allude. The calculation of I and its components and the relationship of I to fitness and to sexual selection have evoked considerable disagreement, in part because the indices do not formally constitute models relating life-table entries of age-specific reproductive output to fitness. This may be an issue of detail, but unsettling nonetheless. The practical problems of measuring LRS, which must include parental effects on recruitment and offspring LRS in many cases, and of accumulating sample sizes large enough to detect patterns amid the considerable stochastic and environmentally induced variation, seem overwhelming for all but the most amenable systems.

The degree to which LRS elucidates evolution depends on its heritability. The two studies in *Reproductive Success* that estimated heritabilities of components of LRS suggest disappointingly small values. Given time, evolution can and probably often does work with small selection differentials and low heritabilities, certainly below the limits of detection in field systems. Life-history theory tells us that negative covariances between fitness components generally constrain phenotypic evolution; the meager evidence for such correlations underscores the difficulty in detecting the general design rules for the architecture of life histories. Most variation appears to be irrelevant to evolution.

Lifetime reproductive success may provide the best measure of fitness, but is it a practical goal for field studies? Clutton-Brock and many of the contributors to *Reproductive Success* suggest that the answers to many questions will ultimately depend upon focused, experimental studies that effectively isolate one or several components of fitness. But because age-dependence figures prominently in most life tables and merits attention in itself, longitudinal studies will, as Clutton-Brock emphasizes, continue to offer unique insights.

Finally, Grafen provocatively asks, What are we interested in? He distinguishes two meanings of adaptation—the process and the result (of processes working in the past)—and suggests that while estimates of I can reveal present-day selection, they cannot explain present-day adaptations. The point is well taken, but the contrast requires further resolution. The end point of evolution depends upon the beginning point (phylogenetic effect) and its subsequent course. Evolutionary response depends upon selection and heritability (including genetic covariation). Thus, present-day selection/response and present-day adaptations (both themes of this book) may be uncoupled by phylogenetic history, environmental change, depletion of genetic variation, altering of genetic and phenotypic covariation, and weakening of selection by achievement of evolutionary optima. These sobering realities might discourage the weakhearted, but *Reproductive Success* has greatly helped to clarify goals and convince skeptics that field studies can elucidate the evolutionary process.

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Loci of Invention

The Sources of Innovation. ERIC VON HIPPEL. Oxford University Press, New York, 1988. xii, 218 pp. $27.

Technological innovations can yield economic benefit for their users, for the firms that manufacture and sell them as products, and for firms whose products they complement. The central argument of this book is that innovation, defined as the first reduction to useful practice of a new or improved technology, is most likely to occur at the locus where the profit (or more precisely, economic rent) captured by the innovator is largest. When product manufacturers in particular are unable to appropriate significant profits from innovation because of weak patent protection, easily copied know-how, or the absence of other barriers to imitation, users are apt to displace manufacturers as innovators.

This thesis is explored through case studies of original and improvement innovations in three classes of scientific instruments (gas chromatographs, nuclear magnetic resonance spectrometers, and electron microscopes), tractor shovels, engineering plastics and plastic additives, wire termination equipment, equipment utilizing industrial gases as an input, the manufacture of semiconductors and printed circuits, and the production of reinforced fiber (for example, epoxy-fiberglass) tubes and related shapes. A third of the book comprises illuminating histories of these innovations; the rest is more analytically structured. Subthemes include know-how trading, particularly among operators of steel mini-mills, and how would-be innovators can exploit the insights of "lead users" (for example, firms employing computer-aided methods to design printed circuits) to determine where a need for a new product exists.

The author's analysis is stimulating and for the most part persuasive, although he falls short when he attempts formal tests of hypotheses on how the locus of innovation varies with the extent of rent capture. He can estimate the magnitudes of rents attainable by product makers and users only subjectively, and given that many of his innovation categories were selected to illustrate one or another relatively pure case, there may be a problem of bias in sample selection. The author's methodology is particularly ill suited to support a proposition stated in the book's first paragraph: that, contrary to conventional wisdom, it is often not typical for innovations to be developed by product manufacturers. The two categories in which users rather than manufacturers played the predominant role, scientific instruments and semiconductor process technology, are almost surely atypical. The ability to jury-rig new apparatus is a requisite for professional success among the academic and industrial researchers who used the scientific instruments in von Hippel's sample. Thus, those users were unusually likely first implementors of new device ideas. Similarly, with respect to the semiconductor industry, my linking of 1976–77 U.S. patents to company lines of business showed that R&D in that industry is extraordinarily process-oriented, with 50% of its patents focused on internal process improvements, compared to 26% for all 15,112 patents in the sample (*Innovation and Growth*, 1984). Overall, roughly 95% of industrial R&D and patented invention does occur in manufacturing lines of business, and the vast majority is product-, not process-oriented.

My research nevertheless provides some quantitative support for von Hippel's thesis. Nearly 45% of the patents in my sample covered capital goods—that is, hardware used in production activities. The classification of patented inventions used in that study distinguished between those that had quite specific uses in three or fewer narrowly defined industries and those with widespread or ubiquitous industrial use. Among the specific-use capital goods inventions, fully three-fourths were developed within the industry that would use them. Thus, general-use equipment appears to come from *product* inventions by firms that sell the equipment whereas special-purpose manufacturing equipment is primarily the subject of *process* invention by the firms that will use